

# Nitrogen and calcium additions increase forest growth in northeastern USA spruce–fir forests

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**Abstract:** We determined responses of red spruce (*Picea rubens* Sarg.) – balsam fir (*Abies balsamea* (L.) Mill.) forests to 6 years of nitrogen (N), calcium (Ca), and N + Ca treatments (100, 160, and 260 kg·ha<sup>-1</sup>·year<sup>-1</sup> of N, Ca, and N + Ca, respectively) in New York (NY) and New Hampshire (NH). Forest responses to Ca treatments were also determined in Vermont (VT). Nitrogen treatments increased aboveground net primary production (ANPP) by 33% and 25% above controls in NY and NH, respectively. Similarly, N + Ca treatments increased ANPP by 27% and 28% in NY and NH, respectively. Calcium treatments increased ANPP by 25% and 21% above controls in NY and VT. Calcium treatment did not increase ANPP in NH, suggesting N, but not Ca limitation. Leaf-litter quantity and quality, and soil C and N storage were greater in treated than in control plots. Fine-root mass and production did not differ among treatments. Trees, therefore, assimilated more soil nutrients without increasing root growth in treated plots. Red spruce ANPP, however, declined or remained unchanged in response to N and Ca additions. The equivalent of 68–102 years of anthropogenic N addition to soils changed forest species composition without decreasing ANPP, and Ca additions did not prevent this change.

**Résumé :** Nous avons déterminé la réaction de forêts d'épinette rouge (*Picea rubens* Sarg.) et de sapin baumier (*Abies balsamea* (L.) Mill.) après 6 années de traitements avec de l'azote (N), du calcium (Ca) et des mélanges de N + Ca (respectivement 100, 160 et 260 kg·ha<sup>-1</sup>·an<sup>-1</sup> de N, Ca et N + Ca) dans les États de New York (NY) et du New Hampshire (NH). Les réactions de la forêt aux traitements avec Ca ont aussi été déterminées dans l'État du Vermont (VT). Les traitements avec N ont augmenté la productivité primaire nette aérienne (PPNA) dans les États de NY et du NH de respectivement 33 % et 25 % comparativement aux traitements témoins. De la même façon, le traitement avec N + Ca a augmenté la PPNA dans les États de NY et du NH de respectivement 27 % et 28 %. Le traitement avec Ca n'a pas augmenté la PPNA au NH, ce qui laisse croire à une déficience en N mais pas en Ca. La qualité et la quantité de litière de feuille ainsi que les stocks de Ca et de N étaient plus élevés dans les parcelles traitées que dans les parcelles témoins. La production et la masse de racines fines ne différaient pas selon le traitement. Par conséquent, les arbres dans les parcelles traitées ont assimilé plus de nutriments sans que la croissance des racines augmente. Cependant, la PPNA de l'épinette rouge a diminué ou est demeurée inchangée en réponse aux apports de N et de Ca. L'équivalent de 68 à 102 ans d'apport anthropogénique de N dans le sol a modifié la composition en espèces de la forêt sans diminuer la PPNA et les apports de Ca n'ont pas empêché ce changement.

[Traduit par la Rédaction]

## Introduction

Nitrogen (N) addition often increases forest growth (Binkley and Hogberg 1997; Elvir et al. 2003; Hogberg et al. 2006); however, when N addition is in excess of biotic demand, forest growth is not expected to increase. When N supply consistently exceeds demand, known as N saturation, cation leaching and aluminum (Al) mobilization may decrease forest growth (McNulty et al. 1996; Aber et al. 1998; Nosengo 2003). Excess N will export any exchangeable soil cations, but loss of calcium (Ca) is of particular concern be-

cause trees require large amounts of Ca (Lawrence et al. 1995). This has led to the suggestion that Ca addition may be an appropriate countermeasure to the effects N saturation (Geary and Driscoll 1996; Wargo et al. 2002; Juice et al. 2006).

Mechanisms explaining N saturation are well understood, but it is not clear how important these mechanisms are to any particular forest because site conditions may influence how quickly forests move between N saturation stages (Aber et al. 1997, 1998; Fenn et al. 1998). More specifically, forests with historically high rates of acid deposition,

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forest floor carbon (C) to N ratios  $<28$ , litter N concentrations  $>1.5\%$ , or overly mature conifers are expected to be susceptible to N saturation (Gundersen et al. 1998; McNulty et al. 2005). Forests with large cation exchange capacity (CEC) and large abiotic and biotic N demand are expected to be resistant to N saturation. While we know that these factors are important, we lack an understanding of the magnitude of their effects under field conditions.

The rate at which forests become N saturated is poorly understood and even less is known about the potential for reversing the N saturation process. Calcium addition has been suggested as a tool for reversing the effects of N saturation, but predicting the effects of Ca addition may even be more difficult than predicting the effects of N addition. This is because N sources are well-constrained, but Ca sources appear to vary with soil conditions and tree species (Hamburg et al. 2003; Jandl et al. 2004; McLaughlin and Phillips 2006). Where Ca additions have been made, Ca has improved tree growth in some sites (Moore et al. 2000; Kobe et al. 2002; Juice et al. 2006), but has had no effect in other sites (Nilsen 2001; Sikstrom 2002; Berger et al. 2006). Thus, experimental tests of the effects of N, Ca, and N + Ca additions under a range of conditions are needed to better parameterize the predictions of the N-saturation model (Aber et al. 2003; Christopher et al. 2006).

It was our objective to determine if continued N deposition induces forest decline and whether Ca additions could ameliorate these effects across sites representing differences in vulnerability to N saturation in the northeastern United States. To address this objective, we conducted N and Ca additions in a "sensitive" site; a site with mature red spruce (*Picea rubens* Sarg.) – balsam fir (*Abies balsamea* (L.) Mill.) stands, on soils with low base saturation and historically high rates of anthropogenic N deposition (Cronan and Grigal 1995; Fenn et al. 1998). To place the responses of this forest in the context of less-sensitive forests, we conducted N and Ca additions to younger red spruce – balsam fir stands with relatively low rates of N deposition. We predicted that experimental doubling of annual biogenic N would induce forest decline in the sensitive site, and result in neutral or positive forest growth responses in the less-sensitive sites (*sensu* Aber et al. 1998, 2003). We predicted that Ca additions would ameliorate the potential effects of N saturation and, therefore, induce positive forest growth responses in the sensitive site and have neutral or positive forest growth responses in the less-sensitive sites.

Finally, fine-root production is likely to be an important component of forest response to N deposition, yet insufficient data are available to determine the response of fine-root growth to N deposition (Wargo et al. 2003; Püttsepp et al. 2006). We predicted that, in response to N addition, root mass or productivity would increase in sites where N is a limiting resource and decrease in sites where N addition induces cation deficiencies or aluminum toxicity (Hendricks et al. 2006).

## Materials and methods

### Study sites

Three mature red spruce – balsam fir stands with closed canopies from across northeastern United States were se-

lected to assess the effects of N and Ca additions on forest growth (Table 1) (David et al. 1998; Lawrence et al. 1999; Wargo et al. 2003). The New York (NY) site is located in the Adirondack Park, near the town of Old Forge, southwest of Big Moose Lake. The Vermont (VT) site is located in the northeast of the state in the Groton State Forest. The New Hampshire (NH) site is located in central NH, in the Hubbard Brook Experimental Forest. Nutrient availability (Oa horizon) in the three sites can be summarized as: NY, high N and low Ca; VT, low N and high Ca; and NH, low N and low Ca (Table 1). The stand in NY was older and less healthy than the stands in VT and NH (Table 1). These forest characteristics reflect the intensive logging history in and around NH in the late 19th and early 20th centuries (Foster et al. 1998). Soils at all sites were coarse-loamy, frigid, Spodosols or Inceptisols, with the exception of some Folistis in NH. Soils in the NY site were in the Brayton–Dannemora and Potsdam–Crary associations, which formed in glacial till derived from granitic, sandstone, and some calcareous rock. Soils in the VT site were in the Tunbridge–Lyman association, which was formed on glacial till derived from schist, gneiss, or granite. The VT site is on a granitic pluton and, therefore, not associated with the metamorphosed calcareous rock common in the area. Soils in the NH site have not been mapped in detail, but are similar to the Tunbridge–Lyman–Rock outcrop complex found in other areas of the Hubbard Brook Experimental Forest (Huntington et al. 1988). Wet N deposition rates, stand age, soil  $\text{NH}_4^+ + \text{NO}_3^-$  concentrations, and soil nitrate concentrations in surrounding watersheds suggested that, at the initiation of this experiment, the NY site was near N saturation stage 2 while the VT and NH sites were near stage 1 (Aber et al. 1998; Chen and Driscoll 2004; Inamdar et al. 2004; Lawrence et al. 2004).

The dominant tree species at the three sites were red spruce (37% of the stem density) and balsam fir (34%). Other common tree species were *Betula papyrifera* Marsh. (paper birch, 19%), *Sorbus americana* Marsh. (American mountain-ash, 6%), and *Acer saccharum* Marsh. (sugar maple, 4%). *Acer rubrum* L. (red maple), *Acer spicatum* Lamb. (mountain maple), *Acer pensylvanicum* L. (striped maple), *Betula alleghaniensis* Britt. (yellow birch), *Tsuga canadensis* (L.) Carrière (eastern hemlock), *Pinus strobus* L. (eastern white pine), *Populus grandidentata* Michx. (bigtooth aspen), *Fagus grandifolia* Ehrh. (American beech), and *Carpinus caroliniana* Walt. (American hornbeam) were present, but each comprised  $<1\%$  of stem density.

## Experimental design

### Plot establishment

In 1992, three replicate 30 m  $\times$  30 m plots were randomly assigned to each of four treatment levels: control (control), Ca addition (Ca), N addition (N), or Ca + N addition (Ca + N) in NY and NH (for a total of 12 plots at each site). In VT, only control and Ca treatments were established because of limited space and because a goal of the research was to determine whether growth decline in spruce could be reversed using Ca additions (for a total of 6 plots). Between July 1992 and July 1998, N amendments (100 kilograms of  $\text{NH}_4\text{NO}_3$ -N per hectare per year), Ca amendments (80 kilograms of  $\text{CaSO}_4$ -Ca plus 80 kilograms of  $\text{CaCl}_2$ -Ca

**Table 1.** Descriptions of vegetation and soil traits of the study sites in New York (NY), Vermont (VT), and New Hampshire (NH).

	NY	VT	NH
Location	43°49'N, 74°53'W	44°16'N, 72°17'W	43°55'N, 71°44'W
Aspect	Level	SW	NE
Approximate elevation (m)	550	520	755
Mean annual temperature (°C)	4.7 <sup>a</sup>	6.1 <sup>b</sup>	4.3 <sup>c</sup>
Spruce DBH (cm)	41	29	21
Average age of spruce (years)	175	97	85
Conifer Density (no. live trees·ha <sup>-1</sup> )	822	738	2278
Hardwood Density (no. live trees·ha <sup>-1</sup> )	279	539	985
Proportion of conifer trees	0.75	0.58	0.70
Conifer biomass (Mg·ha <sup>-1</sup> )	86	91	88
Hardwood biomass (Mg·ha <sup>-1</sup> )	208	110	97
Proportion of conifer biomass	0.29	0.45	0.48
Stand vitality index <sup>a,d</sup>	Fair	Good	Good
Annual precipitation (1992–1998) (mm) <sup>b,c</sup>	1248	1089	1459
Wet N deposition (kg·ha <sup>-1</sup> ·year <sup>-1</sup> ) <sup>b</sup>	7.3	7.1	4.9
Oa soil solution (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> , µmol·L <sup>-1</sup> ) <sup>e</sup>	105	10	14
Ca deposition in precipitation (kg·ha <sup>-1</sup> ·year <sup>-1</sup> ) <sup>f</sup>	0.7	0.8	0.6
Extractable Ca saturation (% of CEC) <sup>g</sup>			
Oe + Oa	20	41	25
B (0–10 cm)	3.1	13	—
Forest floor thickness (cm) <sup>h</sup>	24	9	14

<sup>a</sup>From the Northeast Regional Climate Center (NRCC) for Old Forge, New York.

<sup>b</sup>From the NRCC for Montpelier, Vermont.

<sup>c</sup>From the Hubbard Brook Web site (<http://www.hubbardbrook.org/research/research.htm>) for weather stations 6 and 14. Some data used in this publication was obtained by scientists of the Hubbard Brook Ecosystem Study; this publication has not been reviewed by those scientists. The Hubbard Brook Experimental Forest is operated and maintained by the Northeastern Research Station, US Department of Agriculture, Newtown Square, Pennsylvania.

<sup>d</sup>Fair, 10%–50% dieback; good, <10% dieback.

<sup>e</sup>From the Hubbard Brook Web site (<http://www.hubbardbrook.org/research/research.htm>) and David and Lawrence 1996.

<sup>f</sup>From NADP 2000.

<sup>g</sup>From Tilley 2000 and Wargo et al. 2003

<sup>h</sup>From Lawrence et al. 1997.

per hectare per year), and Ca + N amendments were broadcast by hand as commercial grade salts. Applications were made in June, July, and August to each plot in each year.

### Tree biomass

All 4587 trees with a diameter at breast height (DBH) >2.5 cm were inventoried in 1992 and 1998. Trees that grew into the >2.5 cm size-class from the <2.5 cm size-class were not included in the study; therefore, biomass increment may be underestimated. Aboveground tree biomass (Mg dry matter·ha<sup>-1</sup>) was estimated using measures of the DBH and allometric equations of the form  $\text{Mass} = a \times \text{DBH}^b$ , where  $a$  and  $b$  are species-specific constants (Ter-Mikaelian and Korzukhin 1997). Species-specific equations were used for all species except *Sorbus americana*, which was modeled using the allometric equation derived for mountain maple (*Acer spicatum*). Trees that died during the study period were also measured to allow estimation of biomass lost to tree death (i.e., decrement). When applied to dead trees, allometric equations were derated by 15% because these equations assume growth of branches, foliage, and bark.

A second measure of biomass increment was determined from increment cores taken on a subsample of roughly 10% of all trees (459 trees across sites) in 1997. Increment cores

were optically scanned to determine annual growth increment at the University of Munich using WinDENDRO LA2000 software. The biomass determined for each cored tree species in a plot was summed and divided by the proportion of the number of sampled to total live trees in the plot.

### Aboveground litter collection and analysis

Leaf-litter production represents a large proportion of annual productivity and was expected to be especially responsive to treatments. To describe litterfall responses to treatments five litterfall collectors (0.16 m<sup>2</sup>) were placed in each plot in July 1992 and collected monthly until 1999 unless snow prevented site access, typically November to May. Litter was dried to 70 °C, weighed to the nearest 0.01 g, homogenized to <2 mm in a Wiley sample grinding mill, and subsamples were analyzed by combustion analysis for C and N using a LECO CN analyzer. Subsamples of litter collected in 1996 were composited and combusted at 500 °C for 12 h in a muffle furnace. The resulting ash sample was digested in 6 N HNO<sub>3</sub>, diluted, and analyzed for concentrations of Al, Ca, K, Mg, and P using a PerkinElmer inductively coupled plasma optical emission spectrophotometer (Robertson et al. 1999). Additional 5 g subsamples from the 1996 litter collection

were separated by tissue type and washed in 50 mL of acetone. The labile fraction was extracted with a neutral detergent solution (NDS), the hemicellulose fraction was extracted with an acid detergent solution, and the cellulose fraction was extracted with sulfuric acid (Goering and van Soest 1970).

#### *Fine-root biomass and productivity*

Between June 1992 and June 1993, four soil cores were sampled to 40 cm or bedrock every other month from each control plot (Vogt et al. 1998). In July and October 1996, six root cores were extracted from every plot. For each core, soils were extracted, washed, and roots with a diameter <2 mm were sorted into live and dead roots. Roots were dried to a constant weight at 70 °C. Fine-root biomass was calculated on a per hectare basis (Vogt and Persson 1991).

Belowground net primary production (BNPP) was determined from measurements of fine-root biomass using an approach similar to that reported by Santantonio and Grace (1987) where significant changes in live- or dead-root biomass between two sampling periods were summed to produce an estimate of fine-root production using the following equation:  $BNPP = B_{t_2-t_1} + M_{t_2-t_1}$ , where  $B_{t_2-t_1}$  ( $B$  is the biomass) is the difference in live root biomass from two sampling dates ( $t_1$  and  $t_2$ ) that demonstrated significant differences in biomass;  $M_{t_2-t_1}$  ( $M$  = mortality) is the difference in dead-root biomass from the same two sampling dates that demonstrated a significant difference in biomass. Significant differences in root mass were determined between August and December in 1992 and between July and October in 1996. This approach provides a useful estimate of treatment effects on annual fine-root growth at each site, but estimates from this approach should be treated cautiously because they were determined from two sampling dates within the same year and therefore do not reflect annual variations in BNPP.

#### *Aboveground and total net primary production (ANPP and TNPP)*

Two measures of ANPP were made: stand-level ANPP between 1993 and 1997 and species-level ANPP between 1992 and 1998. Stand-level ANPP was calculated on an annual basis by adding estimates of tree biomass determined from allometric equations using tree-ring data, to estimates of leaf-litter production. Stand-level ANPP, therefore, does not provide species-level data or an estimate of decrement. Species-level ANPP was calculated as the difference in tree biomass determined from allometric equations using DBH data in 1998 and 1992. Species-level ANPP, therefore, does not utilize direct measures of leaf-litter production, but does utilize decrement data. Total NPP (TNPP) was estimated for 1996 by adding ANPP and BNPP values for that year.

#### *Soil sampling*

In November 1996, using a PVC tube (5.23 cm inner diameter), four soil samples were removed from each plot for the analysis of soil C and N content. Only the top 5 cm of mineral soil was sampled because this fraction was expected to be most sensitive to Ca and N treatments. Soil samples were cut in 1 cm increments, dried to 105 °C, sieved to <2 mm, and analyzed for total C and N using combustion analysis. Fine soil particles adhering to the coarse fragments

(2 mm <  $x$  < 5 mm) were washed off, and the weight difference was added to the fine soil portion of the soil core. A plot of % C and % N by depth was used to reveal the boundary between the sapric organic (Oa) and A horizons. A value of 15% C was chosen as the cutoff between the Oa and A horizons to prevent the inclusion of any organic material from the Oa horizon.

#### *Statistical analyses*

In all cases, tests were conducted in SAS programming (SAS version 8e, 1999). Model assumptions of normality were tested using the univariate procedure. Where necessary, data were log transformed to meet assumptions of normality but are reported for nontransformed data. For tests of treatment effects, variables at each site (NY, VT, and NH) were analyzed as distinct case studies; a separate model was determined for each site. General linear models (PROC MIXED) for a one-way factorial design were used to evaluate the fixed effect of treatment, with four levels (control, Ca, Ca + N, and N), on BNPP, decrement, and TNPP in 1996 and on ANPP in 1998. Treatment effects on ANPP and litter production, where determined from annual measurements, were tested using PROC MIXED, and data from each year was treated as a repeated measure on the sampling unit and modeled as a split plot in time. A Dunnett adjustment was used to control for experimentwise error, and differences were accepted at the 0.05 level. Differences among treatment means were tested by Fisher's least significant difference test, except where otherwise noted.  $P$  values are presented. For the five cations and Ca/Al ratios measured in leaf litter, a two-way ANOVA design was used to evaluate the fixed effects of treatment, with either two or three levels (control, Ca + N, N, or control and Ca + N or control and Ca, depending on the site), and tissue type, with two levels (leaves or needles; see Table 2). This design was used because data from all treatment combinations were not available. Significant differences in live- and dead-root biomass within treatments but between two sampling periods were tested to calculate BNPP and were determined with  $t$  tests.

## **Results**

### *Aboveground*

#### *ANPP*

Before the application of experimental treatments there were no differences in standing biomass among sets of plots to be treated within NY ( $F_{3,8} = 0.60$ ,  $P = 0.62$ ), NH ( $F_{3,8} = 2.2$ ,  $P = 0.16$ ), or VT ( $F_{1,4} = 1.06$ ,  $P = 0.36$ ; data not shown). There was more standing biomass in NY than NH or VT (Table 1;  $F_{2,27} = 6.1$ ,  $P = 0.007$ ). In contrast to standing biomass, ANPP determined from increment cores and leaf-litter production in control plots was greater in NH ( $6.2 \pm 0.9$  Mg·ha<sup>-1</sup>·year<sup>-1</sup>) than NY ( $4.6 \pm 0.3$  Mg·ha<sup>-1</sup>·year<sup>-1</sup>) or VT ( $4.3 \pm 0.2$  Mg·ha<sup>-1</sup>·year<sup>-1</sup>) (Fig. 1;  $F_{2,19} = 38.9$ ,  $P < 0.001$ ). When decrement was included in estimates of ANPP determined from DBH measurements taken in 1992 and 1998, ANPP was reduced to  $2.6 \pm 0.2$  Mg·ha<sup>-1</sup>·year<sup>-1</sup> in NH,  $1.2 \pm 0.5$  Mg·ha<sup>-1</sup>·year<sup>-1</sup> in NY, and  $0.5 \pm 0.2$  Mg·ha<sup>-1</sup>·year<sup>-1</sup> in VT (Table 3).

In response to treatments, ANPP determined from incre-

**Table 2.** Elemental concentrations in  $\text{mg}\cdot\text{kg}^{-1}$  for senesced leaf (i.e., hardwood leaf) and needle (i.e., conifer needle) litter collected in 1996 in control, calcium (Ca), Ca and nitrogen (N), or N-treated plots in red spruce – balsam fir stands in New York (NY), Vermont (VT), and New Hampshire (NH).

Litter and site type	Al	Ca	Ca:Al	K	Mg	N	P
<b>NY</b>							
Leaves							
Control	35.7±11a	8700±1290a	273±48a	2540±401b	1780±275a	15400±710c	600±72b
Ca + N	29.1±2a	8810±690a	304±22a	3220±292ab	1750±98a	21200±820a	856±17a
N	27.3±1a	8680±559a	318±16a	4000±163a	1750±17a	18900±840b	780±40a
Needles							
Control	65.7±11a	6770±414a	108±14a	1260±19a	537±59a	10200±500b	526±15b
Ca + N	51.0±14a	6520±1240a	134±19a	1310±114a	474±62a	11700±480a	663±31a
<b>VT</b>							
Leaves							
Control	35.9±3a	8550±371b	243±29a	5350±166a	1460±52a	7900±280b	857±76b
Ca	55.4±17a	9960±933a	215±62a	4970±311a	1440±103a	8600±310a	1100±43a
Needles							
Control	58.8±13a	7140±189b	133±26a	1430±110a	523±19a	8500±250a	639±37b
Ca	54.4±12a	9350±687a	200±64a	1290±79a	627±62a	8300±290a	811±64a
<b>NH</b>							
Leaves							
Control	28.4±2ab	5630±290a	201±23a	1610±167b	906±115a	12100±1100b	841±22a
Ca + N	32.1±2a	6360±2500a	210±95a	2500±344a	860±147a	17400±980a	805±154a
N	23.9±2b	5320±632a	226±38a	2100±82ab	985±61a	17000±940a	890±77a
Needles							
Control	44.2±1a	5930±221a	134±6a	1030±143a	468±44a	9700±360b	659±64a
Ca + N	55.1±16a	7480±1290a	154±34a	1550±446a	469±21a	12200±510a	764±51a

**Note:** Values within treatment × element × tissue type combinations followed by different letters were significantly different at the 0.05 level in a Fisher LSD test. Data were not available for all treatment combinations due to technical difficulties.

**Table 3.** Aboveground net primary production of live trees >2.5 cm DBH after the removal of biomass from trees that died, calculated from a 6 year average (1992–1998) for control, calcium (Ca), nitrogen (N), and Ca + N plots in red spruce – balsam fir stands in New York (NY), Vermont (VT), and New Hampshire (NH).

Treatment	Red spruce <sup>†</sup>	Balsam fir <sup>†</sup>	Maple spp. <sup>†</sup>	Birch spp. <sup>†</sup>	Other* <sup>†</sup>
<b>NY (<math>\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}</math>)</b>					
Control	0.93±0.18a	-0.39±0.33c	0.53±0.16ab	0.02±0.82a	0.07±0.05a
Ca	-0.44±0.67b	0.14±0.17b	0.72±0.51a	0.04±0.62a	0.13±0.08a
Ca + N	-0.25±0.25b	0.49±0.25a	0.10±0.01b	1.17±0.51a	0.02±0.02a
N	-0.27±0.20b	0.26±0.06b	0.26±0.41ab	1.18±0.77a	0.14±0.14a
<b>VT (<math>\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}</math>)</b>					
Control	0.31±0.35a	-0.07±0.04b	0.04±0.43a	0.18±0.49a	0.00±0.00a
Ca	-0.21±0.22a	0.02±0.01a	0.07±0.27a	-0.32±0.18b	0.05±0.05a
<b>NH (<math>\text{Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}</math>)</b>					
Control	1.69±0.21a	0.43±0.08b	0.17±0.09a	0.20±0.17b	0.06±0.03a
Ca	1.48±0.31a	0.10±0.10c	0.25±0.15a	1.14±0.39a	-0.02±0.04a
Ca + N	1.21±0.18a	1.03±0.24a	0.47±0.47a	1.11±0.77a	-0.10±0.13a
N	1.74±0.17a	0.32±0.27b	0.14±0.14a	1.45±0.52a	-0.15±0.10a

**Note:** Values from each site × treatment × species combination represent the mean change in biomass for three replicate 30 m × 30 m plots. Values for each species × site combination (e.g., red spruce in NY) followed by the same lower case letter are not significantly different at the 0.05 level by Fisher's LSD.

\*Values represent the mean ± 1 SE.

<sup>†</sup>Other species: *Tsuga canadensis* and *Fagus grandifolia* at NY; *T. canadensis* and *Populus grandidentata* at VT; *Sorbus americana* at NH.

ment cores and leaf litter production was larger in the Ca-, Ca + N-, and N-treated plots than in the control plots in NY (Fig. 1;  $F_{3,31} = 9.34$ ;  $P < 0.001$ ). In NH, ANPP was larger in the Ca + N- and N-treated plots than in the control plots

(Fig. 1;  $F_{3,32} = 6.26$ ;  $P = 0.0018$ ). In VT, ANPP was larger in the Ca-treated plots than in the control plots (Fig. 1;  $F_{1,16} = 10.69$ ;  $P = 0.0048$ ). Estimates of wood and leaf-litter production helped explain stand-level ANPP responses to site

and treatment effects. In NY, wood growth was larger in the Ca-, Ca + N-, and N-treated plots than in the control plots ( $F_{3,32} = 7.96$ ;  $P < 0.001$ ; data not shown). In NH, wood growth was larger in the Ca + N- and N-treated plots than in the control plots ( $F_{3,32} = 6.49$ ;  $P = 0.0015$ ). There were no differences in wood growth between treatments in VT ( $F_{1,16} = 0.64$ ;  $P = 0.56$ ). Leaf-litter production was larger in the Ca + N-treated plots than in the control plots in NY and NH ( $F_{3,55} = 2.7$  and  $2.8$ ;  $P = 0.03$  and  $0.02$ , respectively). In NY, litter production was also larger in the N-treated plots than in the control plots (Fig. 2;  $F_{3,55} = 4.6$ ;  $P < 0.001$ ). In VT, litter production was larger in the Ca-treated plots than in the control plots (Fig. 2;  $F_{1,28} = 4.0$ ;  $P < 0.001$ ).

Treatment effects measured at the stand level were not attributable to all tree species (Table 3). For example, in NH only the birch spp. ANPP was greater in the N-treated plots than in the control plots (Fig. 1). Similarly, in VT, only balsam fir ANPP was greater in the Ca-treated plots than in the control plots. In NY and VT, two species demonstrated growth responses that were in the opposite direction observed for stand-level growth. In NY, red spruce ANPP was greater in the control plots than in the N-treated plots, although stand-level ANPP determined from increment core data (Fig. 1) was less in the control plots than in the N-treated plots. In VT, the birch spp. ANPP was greater in the control plots than in the Ca-treated plots, although stand-level ANPP determined from increment core data (Fig. 1) was determined to be greater in the Ca-treated plots.

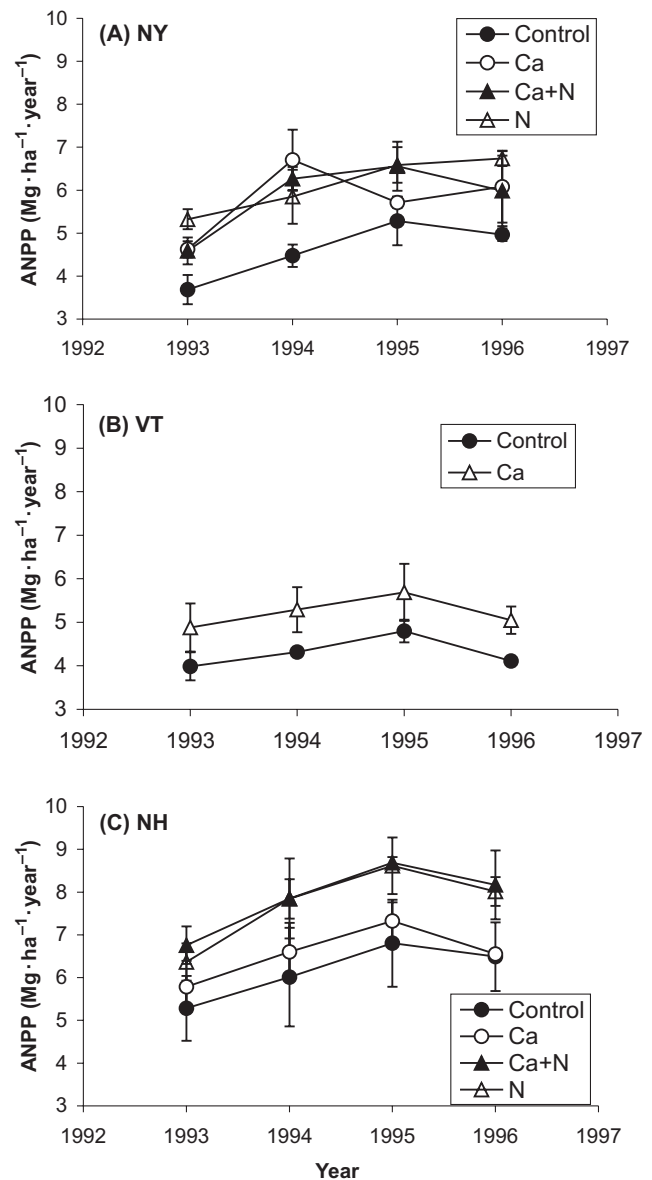
### Leaf-litter chemistry

Collected leaf litter was analyzed for N content between 1993 and 1999, and these values reflected patterns observed with litter mass (Figs. 2 and 3). In NY, leaf-litter N production was greater in the Ca + N- and N-treated plots than in the control plots ( $F_{3,56} = 6.4$ ,  $P < 0.001$ ). In NY, leaf-litter production was also greater in the Ca + N-treated plots than in the control plots ( $F_{3,56} = 4.3$ ;  $P < 0.001$ ). Similar patterns were observed in NH where Ca + N- and N-treated plots produced more leaf-litter N than control plots ( $F_{3,56} = 5.4$ ;  $P < 0.001$ ). Leaf-litter N was also larger in the Ca + N-treated plots than in the Ca-treated plots ( $F_{3,56} = 3.9$ ;  $P = 0.002$ ). In VT, the Ca-treated plots produced more litter N than the control plots ( $F_{1,28} = 4.1$ ;  $P < 0.001$ ).

Across sites, conifer-needle litter had higher Al concentrations ( $\text{mg}\cdot\text{kg}^{-1}$ ) and lower Ca/Al ratios, K, Mg, and P concentrations than hardwood leaf litter ( $F_{1,40} = 22, 22, 59, 110$ , and  $12$ , respectively, and  $P < 0.001$  for each test). Concentrations of all elements analyzed in the hardwood leaf litter differed among sites ( $F_{2,21} = 10, 35, 31, 3.8$ , and  $4.8$  and  $P = <0.001, <0.001, <0.001, 0.04$ , and  $0.02$  for Ca, Mg, K, P, and Al, respectively). Leaf- and needle-litter Al concentrations were greatest in VT, the site with the highest extractable Ca saturation (Table 1). Calcium, K, and Mg concentrations were lowest in NH in hardwood leaves. Phosphorous concentrations were larger in VT than in NY.

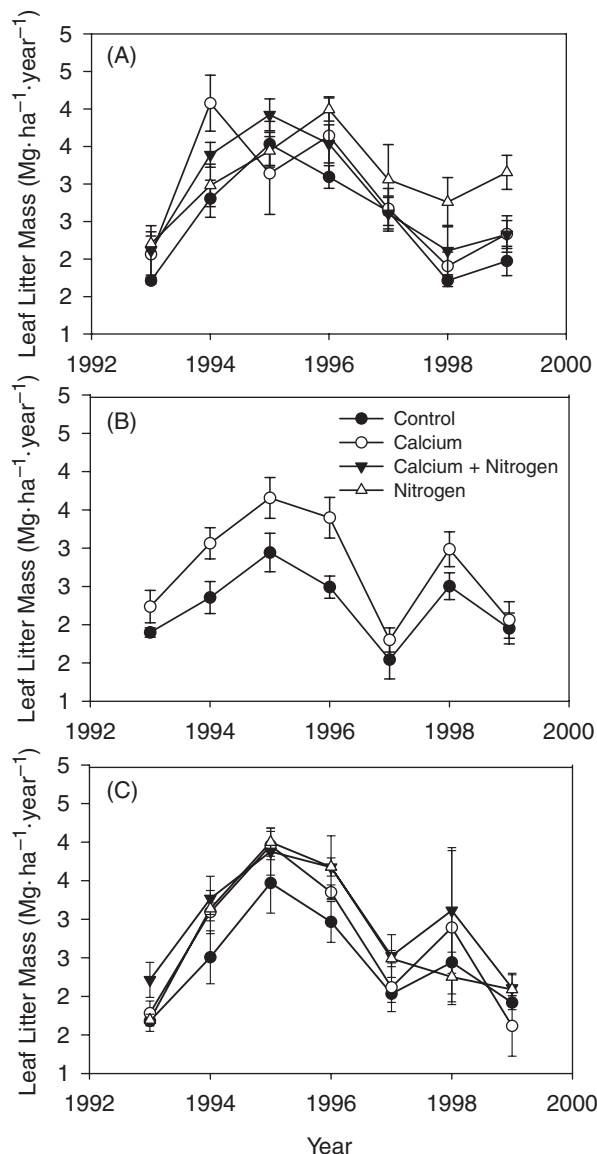
Calcium and P concentrations in hardwood and conifer litter were greater in the Ca-treated plots than in the control plots in VT ( $F_{1,38} = 3.0$ ;  $P = 0.04$  and  $F_{1,38} = 5.5$ ;  $P = 0.003$ , respectively). Potassium and P concentrations were higher in hardwood leaf litter in the N- and Ca + N-treated plots than

**Fig. 1.** Aboveground net primary production (ANPP) in each of three 30 m  $\times$  30 m plots treated as controls (control), calcium treated (Ca), Ca + nitrogen treated (Ca + N), or N treated (N) in (A) New York, (B) Vermont, and (C) New Hampshire. Increment cores removed from 10% of the trees in each plot were used with allometric equations to determine annual wood growth. Five litter collection baskets in each plot were used to estimate annual leaf-litter production. Data from each treatment followed by the same lower case letter were not significantly different at the 0.05 level in a Fisher LSD test when data from each year were treated as repeated measures.



in the control plots in NY and NH (Table 2). Aluminum concentrations were not higher in the N-treated plots than in the control plots in NY or NH ( $F_{2,6} = 0.2$  and  $1.81$  and  $P = 0.82$  and  $0.20$  for leaves in NY and NH, respectively;  $F_{1,4} = 0.85$  and  $0.10$  and  $P = 0.41$  and  $0.76$  for needles in NY and NH, respectively; Table 2). Similarly, the Ca/Al ratio did not differ among treatments for needles or leaves in NY or NH ( $F_{2,6} = 0.60$  and  $0.20$  and  $P = 0.58$  and  $0.82$  for leaves in NY and NH, respectively;  $F_{1,4} = 1.31$  and  $0.18$  and  $P = 0.32$  and  $0.69$  for needles in NY and NH, respectively; Ta-

**Fig. 2.** Annual leaf-litter production during 6 years of treatment applications in spruce stands in (A) New York, (B) Vermont, and (C) New Hampshire. Bars represent the mean and standard error from three replicate 30 m × 30 m plots in each treatment × site combination. Data from each treatment followed by the same lower case letter were not significantly different at the 0.05 level in a Fisher LSD test when data from each year were treated as repeated measures. C, control; Ca, calcium addition; Ca + N, Ca plus nitrogen addition; and N, nitrogen addition.

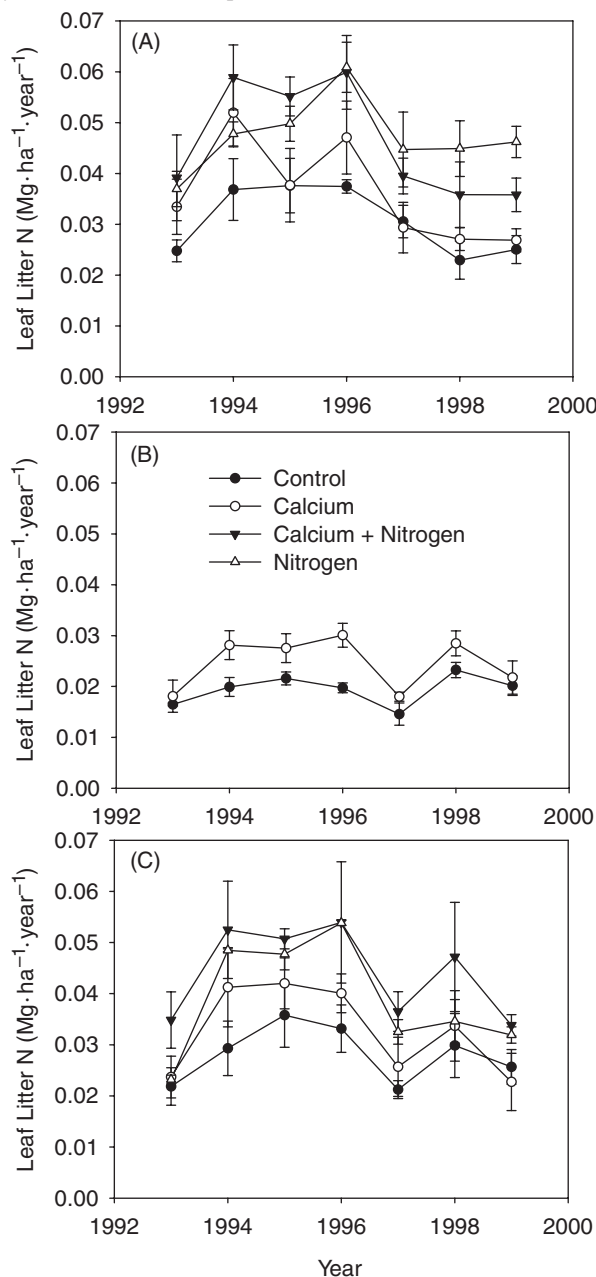


ble 2). To the contrary, Al concentrations in hardwood leaves were lower in the N-treated plots than in the Ca + N-treated plots in NH ( $F_{2,6} = 4.93$  and  $P = 0.05$ ).

#### Leaf-litter fiber fractions

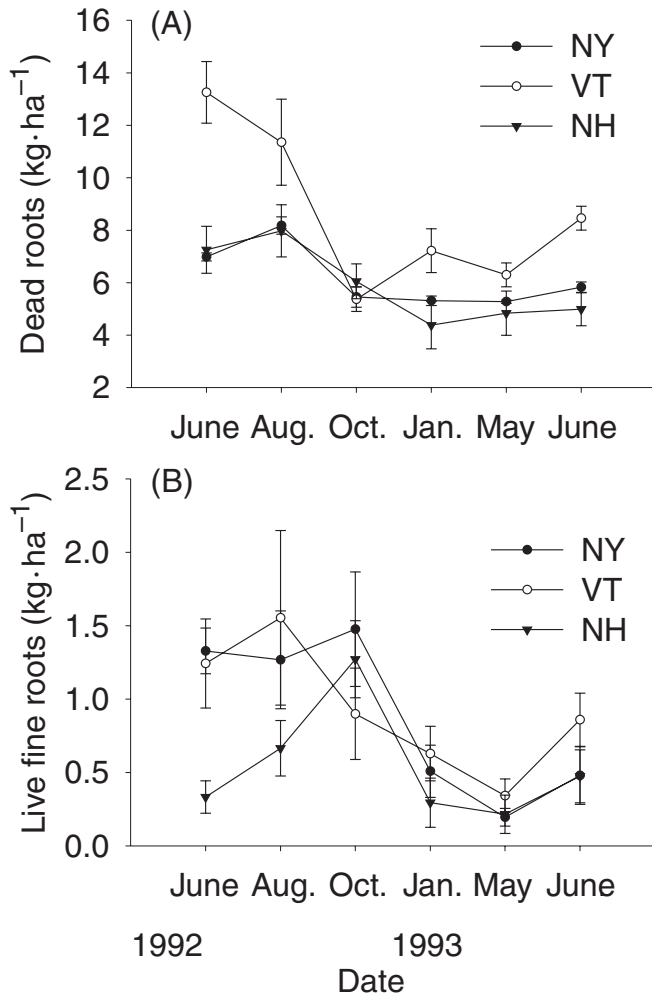
There was weak support for the suggestion that the percentage of hemicellulose in hardwood litter in the N-treated plots in NY was lower than in the control plots ( $7.69\% \pm 3.30\%$  and  $13.8\% \pm 0.54\%$ , respectively;  $F_{2,6} = 3.40$ ;  $P = 0.09$ ), but no other differences in NDS soluble, hemicellulose, cellulose, or lignin fractions were observed for hardwood or conifer litter among experimental treatments. There

**Fig. 3.** Seven years of leaf-litter-nitrogen (N) response to 6 years of control (C), calcium (Ca), nitrogen (N), and Ca + N additions to spruce stands in (A) New York, (B) Vermont, and (C) New Hampshire. Values represent the mean and standard error from three replicate 30 m × 30 m plots in each site. Data from each treatment followed by the same lower case letter were not significantly different at the 0.05 level in a Fisher LSD test when data from each year were treated as repeated measures.



were, however, clear differences in the leaf-litter fiber fractions from different sites and tissue types. Across sites, hardwood leaves contained a larger percentage by mass of NDS soluble materials than conifer needles ( $47.0\% \pm 1.6\%$  and  $24.4\% \pm 0.7\%$  for leaves and needles, respectively;  $F_{1,16} = 86.35$ ;  $P < 0.001$ ) and a smaller percentage by mass of lignin in hardwood relative to conifer needles ( $0.22\% \pm 0.01\%$  and  $0.32\% \pm 0.01\%$  for leaves and needles, respectively;  $F_{1,16} = 28.96$ ;  $P < 0.001$ ). The percent-

**Fig. 4.** Mass of (A) dead and (B) live fine roots between June 1992 and June 1993 in New York (NY), Vermont (VT), and New Hampshire (NH). Values represent the mean and standard error from three replicate 30 m  $\times$  30 m plots in each site.



age of soluble materials in needles did not differ among sites, but there was a higher concentration of soluble materials in hardwood litter in VT ( $53.5\% \pm 0.5\%$ ) than in NH ( $43.9\% \pm 0.5\%$ ) and NY ( $41.4\% \pm 0.04\%$ ) ( $F_{2,6} = 153.37$ ;  $P < 0.001$ ).

## Belowground

### Fine-root mass and productivity

Fine-root mass differed among months, sites, and years (Fig. 4), but not among treatments (data not shown). In 1992, fine, dead-root mass was larger in August than in January in NY ( $F_{4,10} = 3.21$ ;  $P = 0.061$ ), VT ( $F_{4,10} = 9.26$ ;  $P = 0.0021$ ), and NH ( $F_{4,10} = 2.50$ ;  $P = 0.10$ ). Fine, live-root mass also differed among months in VT ( $F_{4,10} = 3.06$ ;  $P = 0.07$ ) and NH ( $F_{4,10} = 6.03$ ;  $P = 0.0098$ ), but not in NY ( $F_{4,10} = 2.27$ ;  $P = 0.13$ ). Differences in fine-root mass among months in 1996 were used to calculate BNPP. Across treatments, BNPP was greater in NH ( $2.95 \pm 0.43 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) than in VT ( $1.80 \pm 0.15 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) and NY ( $1.33 \pm 0.36 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ;  $F_{2,20} = 5.50$ ;  $P = 0.013$ ). No differences

in BNPP were measured among treatments in NY ( $F_{3,8} = 0.31$ ;  $P = 0.82$ ), VT ( $F_{1,4} = 0.63$ ;  $P = 0.47$ ), or NH ( $F_{3,8} = 0.70$ ;  $P = 0.59$ ) (Fig. 5).

### Total net primary production

Total NPP across all treatments was greater in NH ( $9.15 \pm 0.63 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) than in VT ( $6.10 \pm 0.31 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) and NY ( $5.93 \pm 0.42 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) ( $F_{2,27} = 12.62$ ;  $P < 0.001$ ). Total NPP did not respond to experimental treatments in NY ( $F_{3,8} = 1.91$ ;  $P = 0.21$ ), VT ( $F_{1,4} = 1.28$ ;  $P = 0.32$ ), or NH ( $F_{3,8} = 0.18$ ;  $P = 0.90$ ) (data not shown).

### Soil storage

Storage of C and N in the top 5 cm of mineral soil differed among the three sites with the control plots at the VT site storing less C and N than the control plots at the NY or NH sites ( $F_{2,6} = 4.61$  and  $4.88$  and  $P = 0.06$  and  $0.05$  for C and N, respectively; Table 4). In response to treatments, C and N storage increased when the Ca + N treatment was applied to plots in NH ( $F_{3,8} = 2.51$  and  $4.23$  and  $P = 0.078$  and  $0.013$  for C and N, respectively), but not in NY ( $F_{3,8} = 0.88$  and  $1.01$  and  $P = 0.49$  and  $0.44$  for C and N, respectively). Calcium additions had no effect on N storage at any of the three sites (Table 4).

## Discussion

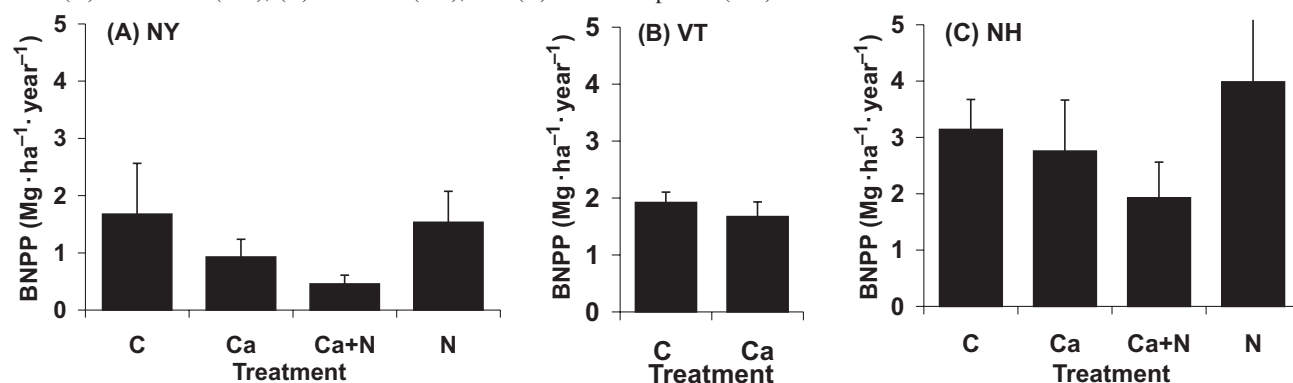
### Forest responses to N treatments

Nitrogen treatments increased ANPP by 1.5 and  $1.6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  in red spruce – balsam fir forests in NY and NH, respectively (Table 3; Fig. 1). Leaf-litter production accounted for  $0.5 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$  of this increase in each site. Nitrogen treatments also increased nutrient assimilation by trees into organically bound pools (e.g., leaf litter). This effect was especially large in NY, where leaf concentrations of N, P, and K were 23%, 30%, and 58% greater in the N-treated plots than in the control plots, respectively. In the same plots where nutrient assimilation increased, root mass and productivity remained unchanged, which is consistent with other studies (Iivonen et al. 2006; Phillips et al. 2006; Püttsepp et al. 2006). Increased nutrient assimilation by trees without increased root growth suggests that N treatments produced a flush of soil nutrients (N, P, and K). Differences in BNPP among sites similarly suggests that root growth declines with N addition, because BNPP was roughly one-half as large in NY relative to NH (Fig. 5).

Our results show that when the equivalent of 68–102 years of atmospheric N deposition is added to the soil, it may not decrease ANPP in young spruce–fir forests with low rates of N deposition or in mature spruce–fir forests with high rates of N deposition (i.e., many northeastern US forests). Furthermore, increased nutrient assimilation into biomass in the N-treated plots could be expected to delay the onset of cation deficiencies. However, productivity in the experimental plots should continue to be monitored because the effects of N saturation may require more than 6 years to observe (McNulty et al. 2005; Hogberg et al. 2006).

Nitrogen treatments did not benefit all tree species. Red spruce ANPP was lower in the N-treated plots than in the control plots in NY (Table 3). There was no evidence that changes in Al concentrations or Ca:Al caused this decline

**Fig. 5.** Belowground net primary production (BNPP) in response to 6 years of calcium (Ca), nitrogen (N), and Ca + N treatments to spruce stands in (A) New York (NY), (B) Vermont (VT), and (C) New Hampshire (NH).



**Table 4.** Total nitrogen (N) and carbon (C) in the 0–5 cm layer of mineral soil in red spruce – balsam fir stands in New York, Vermont, and New Hampshire after 6 years of experimental additions of calcium (Ca), calcium + nitrogen (Ca + N), or nitrogen (N).

Treatment	New York	Vermont	New Hampshire
<b>Mineral Soil N (Mg·ha<sup>-1</sup>)</b>			
Control	0.79±0.07aA	0.50±0.10aB	0.87±0.09bA
Ca	0.69±0.09aA	0.64±0.18aA	0.86±0.12bA
Ca + N	0.68±0.12aB		1.42±0.05aA
N	0.87±0.06aA		1.16±0.25abA
<b>Mineral Soil C (Mg·ha<sup>-1</sup>)</b>			
Control	19.22±1.67aA	11.81±2.37aB	16.35±0.83bAB
Ca	15.91±2.95aA	13.34±0.64aA	18.27±1.76abA
Ca + N	17.16±1.83aB		24.64±0.84aA
N	20.41±1.92aA		20.67±4.39abA

**Note:** Values are mean ± SE of three plots. Treatment means within a site (column) followed by the same lowercase letter are not significantly different at the 0.05 level by Fisher's LSD. Site means within a treatment (row) followed by the same uppercase letter are not significantly different at the 0.05 level by Fisher's LSD.

in spruce growth (Table 2). Reduced red spruce growth also could not be attributed to Ca leaching from needles (McLaughlin et al. 1993; DeHayes et al. 1999) because N was added to the soil surface, or to Ca leaching from soils (Schaberg et al. 2002) because Ca additions did not improve red spruce growth in any site (Table 3). Thus, an explanation other than N-induced Ca deficiency is necessary to explain red spruce declines (Shortle and Smith 1988).

Red spruce may have declined as a result of increased competition from balsam fir and birch spp.; ANPP for these species was greater in the N-treated plots than in the control plots in NY and NH, respectively. Red spruce creates highly acidified, nutrient poor soils in which it is likely able to out-compete other species (Berger et al. 2006), as supported by its low nutrient concentrations in needles relative to hardwood leaf litter (Table 3). It is possible that red spruce loses its competitive advantage where N addition results in a flush of soil nutrients (Tilman 1985).

#### Forest responses to Ca treatments

Calcium treatments increased ANPP in NY, the most N-saturated site, had no effect on ANPP in NH, a less N-

saturated site, and increased ANPP in VT, a site that was not expected to respond positively to Ca additions. Increased ANPP reflected increased wood production in NY and increased leaf-litter production in VT. Calcium treatments did not appear to improve tree growth by reducing Al mobility or the effects of Al-induced Ca deficiencies (Shortle and Smith 1988), because Al concentrations were not lower in Ca-treated plots (Table 2). To the contrary, leaf-litter Al concentrations were greater in the N + Ca-treated plots than in the N-treated plots in NH and greatest in the site with the greatest amount of extractable Ca (VT).

Calcium treatments increased hardwood- and conifer-litter Ca concentrations in VT, the only site they were measured, suggesting that Ca addition may have ameliorated a Ca deficiency. Ameliorating a Ca deficiency, however, was not the only benefit of Ca additions (McLaughlin et al. 1991; Schaberg et al. 2006). We also observed greater P concentrations in hardwood and conifer litter in the Ca-treated plots than in the control plots. Fiorentino et al. (2003) suggested that Ca-SiO<sub>3</sub> addition increases pH, which increases microbial activity and results in greater P-cycling rates. In this study, CaSO<sub>4</sub> and CaCl<sub>2</sub> addition was not expected to increase pH, yet we observed increased P uptake. Two lines of evidence suggest that ion exchange, and not pH, explain increased P-cycling rates. First, we did not observe declines in soil C storage that would suggest increased microbial activity in Ca-treated plots (Huber et al. 2006). Second, P concentrations in hardwood and conifer litter were greater in the N-treated plots than in the control plots in NY, even though NH<sub>4</sub>NO<sub>3</sub> additions were not expected to increase pH. Phosphorus has been suggested to be limiting in N-saturated forests (Gradowski and Thomas 2006). Calcium and N treatments may have increased ANPP in this study by increasing P availability.

Calcium treatments exerted positive or neutral effects on stand-level ANPP, but these effects were not as great as N-treatment effects (Fig. 1). Benefits of Ca addition may be masked if Ca treatments leach Mg out of the soils (Huber et al. 2006); however, there was no indication of a Mg deficiency because Mg concentrations in leaf litter were never lower in the Ca-treated plots than in the control plots. It appears, rather, that stand growth was more limited by N availability than by Ca availability. Forests in Sweden that have received historically high rates of N deposition have

similarly demonstrated smaller tree-growth responses to Ca than to N addition (Sikstrom 2002).

While many studies show positive relationships between soil Ca concentrations and tree growth (Shortle and Smith 1988; Juice et al. 2006), others have failed to observe this relationship or demonstrate experimentally that Ca addition improves tree growth (Jandl et al. 2004; Mellert et al. 2004; Huber et al. 2006). In this study, ANPP was smallest in the site with the greatest Ca saturation (VT), and Ca addition failed to increase ANPP in one of the three sites (NH). Variability in forest responses to Ca addition may be due to differences in local atmospheric or soil Ca supply rates, forest age, tree-species composition, or the physiological responses of individual tree species to changes in cation availability (Hamburg et al. 2003; Bullen and Bailey 2005; Huber et al. 2006).

In a pattern similar to that found for N treatments, Ca treatments decreased the growth of some species. Calcium treatments decreased red spruce ANPP in NY, birch spp. ANPP in VT, and balsam fir ANPP in NH (Table 3). Positive effects of Ca treatments were observed for maple spp. in NY, balsam fir in VT, and birch spp. in NH, supporting findings of Ca deficiency in maple spp., in particular (Juice et al. 2006).

### Forest responses to N + Ca treatments

Nitrogen + Ca treatment responses often reflected the effects of N treatments. For example, ANPP, leaf-litter production, and leaf-litter N were not greater in the N + Ca-treated plots than in the N-treated plots and, therefore, did not reflect the additive effects of the N and Ca treatments (Figs. 1–3). Species-level ANPP responses to N + Ca treatments were similar to both N and Ca treatments: in response to each treatment, red spruce ANPP decreased in both NY and NH, fir ANPP increased in NY, and birch ANPP increased in NH.

There did, however, appear to be an additive effect of N + Ca treatments on soil N and C storage in NH (Table 4). Specifically, N and C storage was greater in the N + Ca plots than in the control, Ca, or N-treated plots. We suspect that increased N storage reflected abiotic and biotic assimilation of experimentally added N and that both increased N and C storage reflected increased leaf litterfall. Interestingly, greater soil C storage is expected to slow the effects of N saturation because it may abiotically immobilize N (Davidson et al. 2003).

BNPP also appeared to demonstrate the additive or synergistic effects of the N + Ca treatments. Small sample size and large variation among plots prevented the detection of statistical differences in BNPP among treatments, but we suspect that intensive sampling would reveal that BNPP decreased in N + Ca-treated plots because BNPP in these plots was less than half that in the control plots in both NY and NH (Fig. 5).

### Nitrogen saturation status

Spruce–fir forests in NY and NH responded positively to large N treatments, yet several conditions suggest that all plots in NY and the N-treated plots in NH could be placed late in N saturation stage 1 (Aber et al. 1998). Hardwood leaf-litter N concentrations were >1.5%, suggesting that net

nitrification was likely in hardwood litter (McNulty et al. 1996). Nitrogen concentrations in leaf litter in NY and NH were double that in VT. Similarly, N concentrations in conifer litter in NY and NH were nearly 50% greater than in VT. Finally, N treatments increased hardwood-litter N concentrations by 26% and 40% above controls in NY and NH, respectively. A 50% increase in litter N concentrations is associated with an increase of nearly one N saturation stage; a doubling is associated with an increase of nearly two stages (i.e., from stage 1 to stage 3) (Aber et al. 1998). Finally, N storage in the top 5 cm of mineral soil was not greater in N or N + Ca-treated plots when compared to control plots in NY, but most of the applied N in N + Ca-treated plots in NH appeared to be retained in the top 5 cm of mineral soil, suggesting that added N leached through the top layers of organic and mineral soil in NY but not NH (Table 4).

Site conditions suggested that the stands used in this study, especially NY, may be sensitive to large N additions, yet experimental N additions induced comparable growth increases in both NY and NH. Our results suggest that tree growth in forests common to the northeastern US remains N limited and that this limitation is greater than Ca limitation. Finally, our results suggest that declines in red spruce growth may reflect shifts in competitive interactions among species under more nutrient-rich conditions induced by N deposition.

### Acknowledgments

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